Nota Lepi. **41**(2) 2018: 225–249 | DOI 10.3897/nl.41.26835

A new species of *Pharmacis* Hübner, 1820 from Spain with a brief review of the genera *Pharmacis* and *Korscheltellus* Börner, 1920 (Lepidoptera, Hepialidae)

Axel Kallies[1], Teresa Farino[2]

1 *University of Melbourne, School of BioSciences, Parkville, 3010 Victoria, Australia; axel.kallies@unimelb.edu.au*

2 *Apartado de Correos 59, 39570 Potes, Cantabria, Spain; teresa.iberianwildlife@gmail.com*

http://zoobank.org/B506D8D1-960D-4267-9140-2B1D8A11F449

Received 25 May 2018; accepted 21 September 2018; published: 9 November 2018
Subject Editor: Maria Heikkilä.

Abstract. We here describe a new ghost moth (Hepialidae) species, *Pharmacis cantabricus* **sp. n.** from the Picos de Europa National Park, Cantabria, in northern Spain. The new species belongs to a group of mostly day-flying species that are restricted to the European Alps and some mountain ranges of southern Europe. Based on morphology and analysis of mitochondrial COI gene sequences, the new species is closely related to *Pharmacis aemilianus* (Constantini, 1911), an endemic of the Italian Apennines. However, *Pharmacis cantabricus* **sp. n.** can easily be distinguished from all related species based on both external and genitalic characters. We briefly review and illustrate all species of the genus *Pharmacis* Hübner, 1820 and discuss its relationship with the related genus *Korscheltellus* Börner, 1920. We reinstate *Hepialus castillanus* Oberthür, 1883 as a distinct species and transfer it to *Korscheltellus* (**stat. rev.**, **comb. n.**).

Resumen. Describimos una nueva especie de Hepialidae, *Pharmacis cantabricus* **sp. n.** del Parque Nacional de Picos de Europa, Cantabria, España septentrional. La nueva especie pertenece a un grupo de especies de vuelo diurno cuya distribución se limita a los Alpes europeos y otras cadenas montañosas de Europa meridional. Según estudios morfológicos y análisis de secuencias del gen mitocondrial COI, la nueva especie es más próxima a *Pharmacis aemilianus* (Constantini, 1911), un endemismo de los Montes Apeninos en Italia. Sin embargo, *Pharmacis cantabricus* **sp. n.** se distingue fácilmente de todas las especies relacionadas en sus caracteres externos y genitales. Evaluamos brevemente e ilustramos todas las especies del género *Pharmacis* Hübner, 1820 y comentamos su relación con el género emparentado *Korscheltellus* Börner, 1920. Restituimos *Hepialus castillanus* Oberthür, 1883 como especie y la trasladamos a *Korscheltellus* (**stat. rev.**, **comb. n.**).

Introduction

The ghost moths (Hepialidae) constitute a family of evolutionarily primitive moths that occur worldwide with >500 species (Nielsen et al. 2000). The family is most species rich in Australia and South America, while in Europe only 15 species are currently known to occur (de Freina and Witt 1990; Leraut 2006). The larvae of most species are borers in or among the roots of woody or herbaceous plants. However, the larvae of some genera outside Europe tunnel in the trunks or branches of shrubs and trees.

In 2007, the second author photographed a mating pair of Hepialidae in the Picos de Europa Mountains in northern Spain that was initially considered to belong to *Korscheltellus fusconebulosa* (De Geer, 1778) (Fig. 1). However, closer inspection showed that the specimens did not conform

to this species and suggested that they may represent a species of the genus *Pharmacis* Hübner, 1820 (type species *Bombyx carna* [Denis & Schiffermüller], 1775). The only *Pharmacis* species currently known from Spain, *P. pyrenaicus* (Donzel, 1838), shows substantial differences in wing pattern and size. Furthermore, *P. pyrenaicus* is limited to alpine habitats in the Pyrenees, usually at altitudes above 2000 m, while the mating pair in the Picos de Europa was found in open oak forest at a much lower altitude of about 800 m (Fig. 2). During subsequent visits to the locality, the authors, with the help of their colleagues Yeray Monasterio León and Ruth Escobés Jiménez, collected a series of males and a female, and confirmed that the specimens belonged to a previously undescribed species of the genus *Pharmacis*. Two further females were located later in the collection of Félix Javier González Estébanez. These had been collected in a different part of the Picos de Europa National Park, in the province of Asturias (Fig. 3). Finally, images of a mating pair and several males were found on Biodiversidadvirtual (2018), suggesting a wider distribution of this species in Cantabria and Asturia or perhaps larger parts of north-western Spain.

In order to place the new species, we review all species of the genus *Pharmacis* and the related genus *Korscheltellus* Börner, 1920, and use morphological and molecular evidence to support species delineation. The results of these studies and the description of the new species, *Pharmacis cantabricus* Kallies & Farino, sp. n., are presented here.

Composition of the genus *Pharmacis*

The genus *Pharmacis* comprises a small group of medium-sized Palaearctic ghost moths. Nielsen et al. (2000) listed eight species in the genus. However, two species were excluded subsequently. Viette (1949) transferred *Phalaena fusconebulosa* De Geer, 1778 to *Korscheltellus*, a view supported by several subsequent authors, including Wagner (1988) and Grehan (2012). This assessment was based on the morphology of a sclerotized ventral extension linked to the pseudotegumen and the fultura superior of the male genitalia. In the past, different authors have interpreted this structure as trulleum (Zilli, 1988) or mesosome (Wagner 1988; Grehan 2012). In agreement with Mielke and Grehan (personal communication), we here interpret it as the ventral extension of the pseudotegumen. It is spatulate and well sclerotized in all three species currently assigned to *Korscheltellus*, including the Palaearctic *K. fusconebulosa* and *K. lupulina* (Linnaeus, 1758) and the North American *K. gracilis* (Grote, 1865). In contrast, it is less sclerotized, distinctly three-dimensional and bears multiple fine ridges in *Pharmacis*. Leraut (2006) placed *Hepialus castillanus* Oberthür, 1883, an enigmatic taxon from Spain, previously assigned to *Pharmacis* by de Freina and Witt (1990) and Nielsen et al. (2000), as a subspecies of *K. fusconebulosa*. However, Leraut did not provide any detailed justification for his assessment. Based on the description and figures of genitalia provided by Agenjo (1942) and our own assessment of a specimen from the type locality, we support the notion that *H. castillanus* is related to *K. fusconebulosa* but conclude that it constitutes a valid species, *Korscheltellus castillanus* (Oberthür, 1883) stat. rev., comb. n. Furthermore, Leraut (2006) transferred *Hepialus nebulosus* Alphéraky, 1889 from Tibet, to *Pharmacis*. Subsequently, however, this taxon was placed in *Parahepialus* Zou & Zhang, 2010 (Zou et al. 2010), now considered a synonym of *Thitarodes* Viette, 1968 (Jiang et al. 2016). Finally, the status of the taxon *Hepialus uralensis* Grum-Grshimailo, 1899, for a long time considered a synonym of *Pharmacis carna*, has recently been clarified. It was reinstated as a *bona fide* species, *Gazoryctra uralensis* (Grum-Grshimailo, 1899) (= *Hepialus fuscoargenteus* Bang-Haas, 1927), by Anikin and Zolotuhin (2017). Thus, at present *Pharmacis* comprises six valid species, which occur exclusively in the Western Palaearctic, while the genus *Korscheltellus* contains four species with a wide Palaearctic and Nearctic range.

Checklist

The considerable list of synonyms and intrasubspecific names linked to some of these taxa can be found in Nielsen et al. (2000).

Pharmacis Hübner, 1820
P. carna ([Denis & Schiffermüller], 1775)
P. claudiae Kristal & Hirneisen, 1994
P. anselminae (Teobaldelli, 1977)
P. bertrandi (Le Cerf, 1936)
P. pyrenaicus pyrenaicus (Donzel, 1838)
P. pyrenaicus alticola (Oberthür, 1881)
P. aemilianus (Constantini, 1911)
P. cantabricus sp. n.

Korscheltellus Börner, 1920
K. fusconebulosa (De Geer, 1778)
K. castillanus (Oberthür, 1883), stat. rev., comb. n.
K. gracilis (Grote, [1865])
K. lupulina (Linnaeus, 1758)

Methods

COI sequences were downloaded from BOLD (http://www.boldsystems.org/index.php/) or generated using the methodology described in detail by Milla et al. (2017). COI sequence alignments were created using the MAFFT v7.3.09 (Katoh and Standley 2013) plugin within Geneious R11.02 (Biomatters Ltd.) using the default Auto option. For the maximum likelihood (ML) analysis, we used the nucleotide substitution model GTR + I + G for RAxML (Stamatakis 2014) and 500 bootstraps. Pairwise sequence differences were calculated using Geneious. Genitalia were examined using standard methods and embedded in Euparal. For detailed examination of the labial palps, they were removed from the head, cleared in ethanol and embedded in Euparal. Antennal segments were counted under the microscope without including the scape. Images are by the authors unless specified differently.

Results of molecular analysis

In order to place the new species confidently within the genus *Pharmacis* and to test whether currently recognized species in the genus were supported by molecular data, we utilized mitochondrial COI DNA barcodes. Analysis of the COI sequences revealed that all species analysed in this study formed well separated monophyletic entities, supporting the notion that they are valid taxa (Fig. 4). *Pharmacis cantabricus* sp. n. was resolved as a sister species to *P. aemilianus*, and the pair formed a sister clade to the rest of the *Pharmacis* species with the exception of *P. pyrenaicus*. *Pharmacis claudiae* was placed as a sister to a clade consisting of *P. carna*, *P. anselminae* and *P. bertrandi*, the latter two being sister species. Within the genus, the pairwise sequence difference was between 2% and 2.7% for sister species (*P. cantabricus* sp. n. *vs P. aemilianus*, and *P. an-*

selminae vs P. bertrandi) and 4.6% for more distantly related species (*P. cantabricus* sp. n. *vs P. carna*). Notably, *P. pyrenaicus* grouped together with species of *Korscheltellus*. However, although *P. pyrenaicus* is very distinct from the other *Pharmacis* species, both with regards to genitalia and antennal structures, there is little if any morphological evidence to support a close association with *Korscheltellus*. Overall, while our data support all taxa as valid species, more extensive molecular and morphological analyses are required to resolve the systematic position of *P. pyrenaicus* and the phylogeny of the genera *Pharmacis* and *Korscheltellus*.

Distribution, behaviour and biology of *Pharmacis*

Species of the genus *Pharmacis* occur in the mountains of central, southern and south-western Europe, with one species, *P. carna*, also occurring in Fennoscandia. Some of the species show an extremely limited distribution, including *P. bertrandi*, *P. anselminae* and *P. claudiae*, which occur exclusively in small, high-altitude areas in the French and Italian Alps. Although both *P. pyrenaicus* and *P. aemilianus* have larger ranges, they too are restricted to relatively small regions covering the Pyrenees and Abruzzi, respectively. Notably, several of the *Pharmacis* species, including *P. anselminae*, *P. bertrandi* and *P. pyrenaicus*, have brachypterous females, probably an adaptation to the harsh conditions of the alpine environment in which they occur. Two of these species, *P. anselminae* and *P. pyrenaicus*, appear to be strictly day-flying, a feature shared by many moths that occur in alpine environments or high latitudes. The third species with brachypterous females, *P. bertrandi*, was found to be active in the second half of the night and in the morning. In contrast, *P. claudiae* and *P. aemilianus* have fully winged females and fly during the night time. *Pharmacis carna* on the other hand occurs from the foothills to the alpine regions of the Alps and other mountain ranges. It has been observed at night in some areas, whereas it was found to be active predominantly during the day in other areas (Daniel 1950; Wenta, personal communication). Thus, *Pharmacis* species associated with the higher mountain ranges of Europe show distinct morphological and behavioural adaptations to their environment. The larvae of *Pharmacis* species are underground feeders that appear to utilize the roots of a broad range of grasses and herbaceous plants (de Freina and Witt 1990; Buser et al. 2000; Leraut 2006).

Abbreviations. MfN – Museum für Naturkunde, Berlin, Germany; IBEB – Institut de Biologia Evolutiva, Barcelona, Spain; ZSM – Zoologische Staassammlung, München, Germany; CAK – collection A. Kallies, Australia; CAM – collection Anton Mayr, Austria; CEF – collection Egbert Friedrich, Germany; CFG – collection Félix Javier González Estébanez, Spain.

Taxonomy

Pharmacis cantabricus sp. n.

http://zoobank.org/BB7AEA86-EDB8-4096-8914-71CA2D02FF8F

Figs 1, 5–8, 29–32, 39, 41, 46

Type material. Holotype (Fig. 5): 1 ♂, N Spain, Cantabria, Picos de Europa National Park, Sierra de Bejes, ca 800 m, 43.247N, 4.651W, 9. July 2016, day flying, leg. A. Kallies & T. Farino (CAK, in MfN). Paratypes: 2 ♂, same data as holotype (genitalia prep. AK790, Figs 6, 39, 46); 7 ♂, 1 ♀, same locality, 18. July 2017, day flying, leg. Y. Monasterio, T. Farino & R. Escobés (CAK, specimens will be lodged in MfN, ZSM and IBEB, Figs 7, 29–

Figures 1–3. 1. *P. cantabricus* sp. n., mating pair, Spain, Cantabria, Picos de Europa, Sierra Bejes. **2.** Type locality of *P. cantabricus* sp. n. at the Sierra Bejes at about 800 m altitude. **3.** Habitat of *P. cantabricus* sp. n. above the Lagos de Covadonga, at about 1375 m altitude. Image **3**, F. González.

32); 2 ♀, N Spain, Asturias, Picos de Europa National Park, Lagos de Covadonga, ca 1375 m, 43°14'37.10"N, 4°59'44.23"W, 20. July 2007, during the day, leg. F. J. G. Estébanez (CFG, genitalia prep. AK861, Figs 8, 41).

Description. ***Male*** (Figs 5, 6, 29, 30, 39, 46). Alar expanse 29–33 mm, forewing length 13–15.5 mm. Head and thorax ochre-brown to greyish, covered with soft and relatively long, hair-like scales. Scales between eye and antenna present. Antenna consisting of 30–31 segments that are short, wide and relatively flat, resulting in an overall flattened (lamellate) antenna morphology. Labial palps well-developed, protruding well beyond the frons; three-segmented, with the three

palpomeres well separated, the middle palpomere about twice as long as the apical one, the apical palpomere globular; dorsally with short scales, ventrally with long, hair-like scales. Forewings dark brown, along the costa and the area of the radius suffused with light ochre-brown; with an ill-defined whitish streak close to base; with an irregular white patch anterior of vein A; with another white patch between veins A and CuA2 near the anal angle, sometimes extending to the area between CuA1 and CuA2; with a few very small, ill-defined white patches postmedially; with a small white spot in the area of the cell at the stem of M2 and another small white spot at the basal fork of M1; all white markings embedded into light brown areas. Hindwing uniformly dark brown. Fringes of both fore and hindwing short and uniformly dark. Fore tibia with a distinct epiphysis, which consists of an open tube-like structure, ending in a short and wide tooth. Abdomen dorsally ochre to grey, ventrally light ochre, posterior margins of tergites light ochre. Abdominal sclerites (Fig. 46) poorly sclerotized, tergites 7 and 8 simple, sternite 7 laterally with a membranous spot on each side; sternite 8 roughly triangular and relatively long.

Female (Figs 7, 8, 31). Alar expanses 30–35 mm, forewing length 15–17.5 mm. Similar to male, but wings narrower, with 26–29 antennal segments, the extent of the white forewing markings variable. The white forewing markings of the female paratype from the type locality are extensive and similar to the markings of the males from the same location. However, the female photographed at the same location (Fig. 1, right specimen) has reduced white marks. One female from the Lagos de Covadonga lacks any distinct white markings (Fig. 8).

Male genitalia (Fig. 39). Vinculum with long processes (vincular condyles *sensu* Grehan 2012) at posterior margin; saccus rounded; the paired apical processes of the pseudotegumen long, each with a small protrusion at the distal margin, not fused; ventral extension of the pseudotegumen (trulleum *sensu* Zilli 1988 and Simonsen 2018; spatulate mesosome *sensu* Wagner 1988 and Grehan 2012) large and well sclerotized; valva relatively straight, long and narrow, without sub-basal tooth at the ventral margin.

Female genitalia (Fig. 41). Papillae anales narrow and setose; lamella antevaginalis shortly setose, with two submedial invaginations forming ventricle-like structures; each a very small sclerotized plate on either side of the ostium; corpus bursae ovoid, membranous; ductus bursae long and simple.

Variability. *Pharmacis cantabricus* sp. n. shows considerable variability in the extent of the white markings on the forewing. Specifically, the spots between A and CuA2 can be reduced or confluent, the white streak in the base of the forewing can be more or less extensive. Similarly, the extent of the light brown areas of the forewing varies. The female of a mating pair figured on Biodiversidadvirtual (2018, as *Pharmacis* sp.) has dark grey instead of brown forewings. The corresponding male is ochre-brown, and both specimens have the white mark reduced to the discal spot. In some females the white marks can be absent altogether (Fig. 8).

Diagnosis. Males of *P. cantabricus* sp. n. can be differentiated from males of all other species by the white forewing markings, which are usually reduced to an often ill-defined white streak near the base, an irregular white patch just anterior of vein A, and a third white patch between veins A and CuA2 near the anal angle. The extent of these white markings is, however, variable. In some specimens they are further reduced or even absent (as in the female in Fig. 8), in others they form an almost continuous white line (as in female in Fig. 7). *Pharmacis cantabricus* sp. n. differs from most other species of *Pharmacis*, with the exception of *P. aemilianus*, by the well-developed labial palps. Although the labial palps of all *Pharmacis* species consist of three segments, they markedly

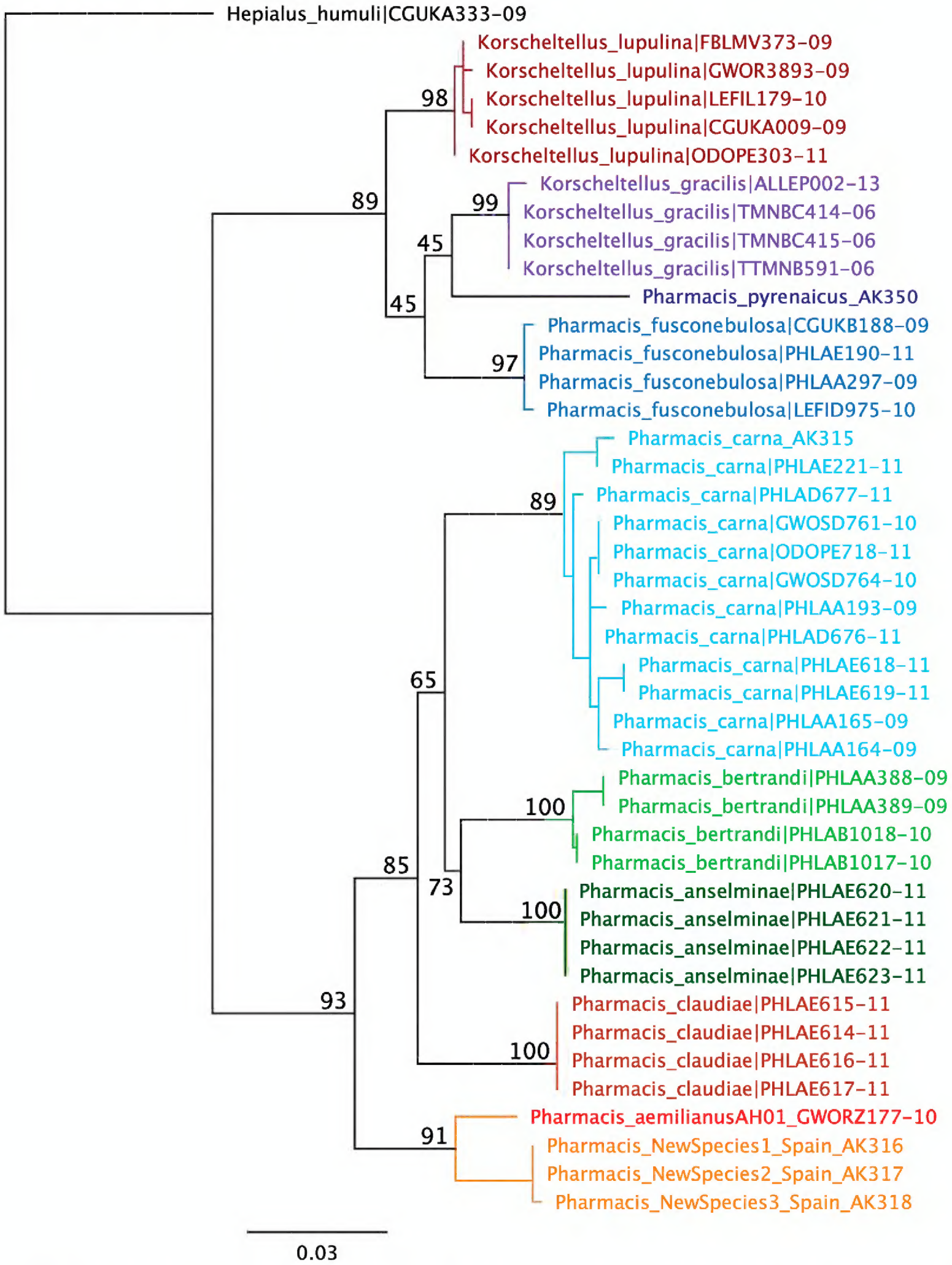


Figure 4. Maximum likelihood (ML) tree inferred from COI sequences for the genera *Pharmacis* and *Korscheltellus*, with the outgroup *Hepialus humuli*. Branch lengths are proportional to ML estimated branch lengths. Values above the branches are percentage of ML bootstrap supports.

differ in their structure. In *P. cantabricus* sp. n. all segments are well-separated, and while the middle palpomere is very long, the apical palpomere is very short and distinctly bulbous. In all other species, with the exception of *P. aemilianus*, the labial palps are much shorter, and the palpomeres are of similar length, with the apical one pointed and partially fused to the middle segment. Furthermore, in *P. cantabricus* sp. n. and *P. aemilianus*, the labial palps are covered with short scales dorsally and long and thin scales ventrally, while they are clothed in long hair-like scales dorsally and ventrally in all other species. Diagnostic characters can also be found in the abdominal sclerites, which are poorly sclerotized in *P. cantabricus* sp. n. (Fig. 46) and *P. aemilianus* (not shown), while they are well sclerotized in the other species examined, *P. anselminae* (Fig. 47) and *P. pyrenaicus* (Fig. 48). Sternite 7 is relatively wide in *P. cantabricus* sp. n. and *P. aemilianus* while it is narrow in the distal half in other species examined (*P. pyrenaicus* and *P. anselminae*). Sternite 8 is roughly triangular and relatively long in *P. cantabricus* sp. n. and *P. aemilianus*, while it is quadrangular and short in *P. anselminae* (Fig. 47) and very wide and short in *P. pyrenaicus* (Fig. 48).

Based on DNA barcoding, morphology of the genitalia and labial palps and the number of antennal segments, the new species appears to be closely related to *P. aemilianus* (Figs 9, 10) from Italy. Both species have about 29–30 antennal segments, well-developed labial palps and a well-developed ventral extension of the pseudotegumen of the male genitalia. However, these two species can be easily separated by external characteristics such as wing coloration (yellow-brown to ochre-brown in *P. aemilianus*; dark brown with light brown markings in *P. cantabricus* sp. n.), white forewing markings (typically reduced and often with just a white mark prominent in the cell in *P. aemilianus*; typically with larger white markings along the posterior section of the forewing in *P. cantabricus* sp. n.), the size (substantially larger, alar expanse in males 30–36 mm and in females 36–52 mm in *P. aemilianus*), and wing shape (in *P. aemilianus* the forewings longer and narrower in males, broader in females). The genitalia of both species are very similar. Males of both species display a well-developed ventral extension of the pseudotegumen and large vincular condyles. Similarly, the ventricle-like invaginations in the lamella antevaginalis of the female genitalia is present in both species. However, *P. cantabricus* sp. n. differs from *P. aemilianus* in a number of details: the apical part of the valva is shorter and narrower in *P. cantabricus* sp. n. (longer and expanded in *P. aemilianus*), the paired ventral processes of the pseudotegumen are longer, and the apical margins of pseudotegumen have a small protrusion (absent in *P. aemilianus*), the saccus is more rounded (tapering to a point in *P. aemilianus*) and the processes of the vinculum are tapering and bent outwards (wider and bent inwards in *P. aemilianus*). Furthermore, both species differ in their behaviour, with *P. aemilianus* being active at dusk and during the night, whereas *P. cantabricus* sp. n. appears to be strictly day-flying. Finally, females of *P. aemilianus* are able to fly freely, which does not appear to be the case for female *P. cantabricus* sp. n.

Pharmacis pyrenaicus (Figs 11, 12, 35) can easily distinguished by the light yellow to white fringe of the hindwings (uniformly dark in *P. cantabricus* sp. n.) and the usually much more extensive white markings of the forewings. Furthermore, the males of both species differ in their antennae, which are not flattened, appear somewhat serrate and have only 22–23 segments in *P. pyrenaicus*. Both species also differ profoundly in their male genitalia. The ventral extension of the pseudotegumen and projections at the posterior margin of the vinculum are absent, the valva is short and arched, and the saccus is square in appearance in *P. pyrenaicus*. Finally, the female of *P. pyrenaicus* (Fig. 35) is brachypterous, while the female of *P. cantabricus* sp. n. is fully winged. *Pharmacis bertrandi* (Figs 13, 26) has very regular and extensive white forewing markings, usu-

Figures 5–12. *Pharmacis* species. **5–8.** *P. cantabricus* sp. n., Spain, Picos de Europa. **5.** Male, holotype, alar expanse 33 mm (MfN). **6.** Male, paratype, alar expanse 30 mm. (CAK). **7.** Female, paratype, alar expanse 31 mm (CAK). **8.** Female, paratype, alar expanse 35 mm (CFG). **9–10.** *P. aemilianus*, Italy, Abbruzi, Pesco-costanzo. **9.** Male, alar expanse 34 mm (MfN). **10.** Female, alar expanse 52 mm (MfN). **11.** *P. pyrenaicus pyrenaicus*, male, France, Pyrenees, alar expanse 25 mm (CAK). **12.** *P. pyrenaicus alticola*, male, Pyrenees, alar expanse, 27.5 mm (MfN).

Figures 13–18. *Pharmacis* species. **13.** *P. bertrandi*, male, Italy, Cuneo, alar expanse 38 mm (CAM). **14–16.** *P. carna*. **14.** Male, Austria, Oberösterreich, alar expanse 33 mm (CEF). **15.** Male, Austria, Steiermark, alar expanse 35 mm (CEF). **16.** Female, Italy, Lombardia, alar expanse 40 mm (CAK). **17.** *P. anselminae*, male, Italy, Valle de Aosta, alar expanse 33 mm (CAK). **18.** *P. claudiae*, male, Valle de Aosta, alar expanse 41 mm (CAK). Images **13**, H. Deutsch; **14–15**, E. Friedrich.

ally also in the termen and close to the costa, markedly embedded into reddish brown areas (reduced white markings, absent in the termen and costal area in *P. cantabricus* sp. n.). Males have 34–35 antennal segments. Females of *P. bertrandi* are brachypterous. *Pharmacis carna* (Figs 14–16, 27, 33) has more extensive yellow to white forewing markings; the hindwing fringe is mixed yellow and dark brown (dark brown throughout in *P. cantabricus* sp. n.). Males have 25–27 antennal segments (Buser et al. 2000 and our observations). Females of *P. carna* are fully winged and able to fly. *Pharmacis anselminae* (Figs 17, 25, 34) differs substantially by the light

Figures 19–24. *Korscheltellus* species. **19–21.** *K. fusconebulosa*. **19.** Male, Italy, Vintschgau, alar expanse 36 mm (CEF). **20.** Male, Germany, Schmalkalden (CEF). **21.** Female, Germany, Schmalkalden (CEF). **22.** *K. castillanus*, female, alar expanse 32 mm (MfN). **23–24.** *K. lupulina*. **23.** Male, Germany, alar expanse 27 mm (CEF). **24.** Female, Austria, Steiermark, alar expanse 33 mm (CAK). Images **19–21**, **23**, E. Friedrich.

markings on its forewing, which are not distinctly edged or embedded into light brown scales, and by the presence of a dirty yellow patch subapically at the forewing costa. Males have 25–27 antennal segments (Buser et al. 2000). Females of *P. anselminae* are brachypterous. *Pharmacis claudiae* (Fig. 18) has extensive and evenly distributed white markings on the forewings (reduced in *P. cantabricus* sp. n.) and the hindwing fringe is white, somewhat mixed with dark brown at the veins. Males have 26–28 antennal segments (Buser et al. 2000). Females of *P. claudiae* are fully winged and able to fly.

Finally, *P. cantabricus* sp. n. differs from all species of *Korscheltellus* in the shape of ventral extension of the pseudotegumen (spatulate and simple in *Korscheltellus*, three-dimensional and furrowed in *P. cantabricus* sp. n.) and the forewing pattern. From both *K. fusconebulosa* and *K. castillanus* stat. rev., comb. n. the new species also differs by the monochrome brown fringes of fore and hindwings (chequered in the two species compared).

Habitat and biology. *Pharmacis cantabricus* sp. n. inhabits open grassy woodlands and rich meadows and pastures in montane and subalpine parts of the Picos de Europa. In the Sierra de Bejes, the authors found *P. cantabricus* in open *Quercus petraea* (Matt.) Liebl. woodland with *Corylus avellana* L. on a north-west-facing ridge of Carboniferous limestone at about 800 m altitude (Fig. 2). The ground layer is dominated by *Brachypodium* P. Beauv. species, with accompanying *Aquilegia vulgaris* L., *Geranium sanguineum* L., *Astrantia major* L. and *Thalictrum minus* L. Here, *P. cantabricus* sp. n. shares its habitat with *Lopinga achine* (Scopoli, 1763) (Nymphalidae) and *Carterocephalus palaemon* (Pallas, 1771) (Hesperiidae), two butterfly species with a very restricted distribution in Spain.

The second known locality is considerably different. It is situated above the Lagos de Covadonga at about 1375 m (Fig. 3). Here the specimens were found in open pastures interspersed with limestone outcrops, used for cattle grazing (Estébanez, personal communication). Another mating pair was photographed by Antonio Rodriguez at low altitude (<200 m) west of the Picos de Europe on the 30th of July 2016 (Biodiversidadvirtual, 2018; as '*Pharmacis* sp.'). Finally, specimens that may belong to *P. cantabricus* sp. n. were observed by Marcos Toribio in Robledo de Anayo (Asturia) at about 550 m altitude (Biodiversidadvirtual, 2018; as '*Pharmacis lupulina*'). These specimens were attracted to lights over several days in early September 2014 (Toribio, personal communication). However, there were no specimens available to conclusively test their identity. Thus, while confirmed records suggest that *P. cantabricus* sp. n. is limited to the Picos de Europa and flies only during the day in July, additional unconfirmed records suggest that it may fly well into September and may also be active at night.

Males of *P. cantabricus* sp. n. were seen flying rapidly over the vegetation between the late morning and afternoon. Mating was observed in the afternoon. Detailed observations were made in the Sierra de Bejes on the 18 July 2017. On arrival at the site at 12.45 pm, the weather was sunny, 24 °C, with light winds. The cloud cover was 40–50% initially, but increased to about 90% by 4.40 pm, with only a few sporadic sunny intervals later. A total of 7 males were caught between 1.35 and 5.05 pm. One male was caught at 3.00 pm, when it was attracted to a female hanging in grasses by the side of the track (Fig. 31), although it made no attempt to copulate. The female was then placed in a cage. Her abdomen, although bulky, was not extended much below the wings in resting posture at this point. At 5.00 pm, two males were placed in the cage with the female. Shortly after this, copulation took place, which lasted less than 35 minutes (Fig. 32). During mating, the abdomen of the female became much more extended (compare Fig. 1). By approximately 6.30 pm the female had laid a copious quantity of eggs and her abdomen had shrunk considerably. On one occasion, on the 9 July 2016, on the same day when multiple males were observed flying during day time, light trapping was undertaken at the type locality. However, no specimens were attracted to the light, suggesting that the main period of activity is during the day. This notion is also supported by the observation that mating occurred in the afternoon.

Distribution. The new species is currently known only from a small area that includes the Picos de Europe and the surrounding area in the provinces of Asturia and Cantabria in north-western Spain.

Figures 25–31. Live *Pharmacis* specimens. **25.** *P. anselminae*, male, Italy, Valle de Aosta. **26.** *P. bertrandi*, male, France, Haute Alps. **27.** *P. carna*, male, Poland, Tatra Mts,. **28.** *P. aemilianus*, male, Italy, Central Apennines. **29–31.** *P. cantabricus* sp. n., males (**29, 30**), female (**31**), Spain, Picos de Europa. Images **25**, R. Bryner; **26**, A. Longieras; **27**, J. Wenta; **28**, P. Mazzei.

Discussion

The highly restricted distribution of most of the *Pharmacis* species is probably a result of frequent glaciation events during the Pleistocene or earlier ice ages. During these periods, *Pharmacis*

populations may have withdrawn into isolated refugia in the mountains of southern Europe and undergone speciation. Such a scenario is exemplified by the distribution of the three species of the *P. carna* species group (*P. anselminae*, *P. bertrandi* and *P. claudiae*), each of which is represented by small isolated populations in the French and Italian Alps. The hypothesis of glaciation-driven speciation in *Pharmacis* may be supported by the relatively low pairwise sequence differences between closely related species (2–2.7%) observed here. Based on the estimated 1.0–2.3% per million years (Mya) average substitution rate for COI (Kandul et al. 2004; Wilke et al., 2009), these values suggest that *Pharmacis* diversification was initiated during the early pleistocene glaciation periods, which commenced about 2.58 Mya. The initial split between the clade containing *P. aemilianus* and *P. cantabricus* sp. n. and the rest of *Pharmacis* is likely to have occurred much earlier given the pairwise difference of 4.6% between *P. cantabricus* sp. n. and *P. carna*. However, estimates of the age of speciation events based on COI sequence differences are controversial as the rate of evolution of COI is thought to be taxon dependent (Pentinsaari et al. 2016).

The new species, *P. cantabricus* sp. n., is currently known only from within and around the Picos de Europa, a small mountain range at the convergence of the provinces of Asturias, Cantabria and León in northern Spain. In contrast to the high alpine environment inhabited by other highly localized *Pharmacis* species, *P. cantabricus* sp. n. was found in open oak (*Quercus*) woodland in the montane zone and in subalpine pastures. However, additional observations suggest that it also occurs at much lower altitude, and it remains to be seen how widely *P. cantabricus* sp. n. is distributed in northern and north-western Spain. *Pharmacis aemilianus*, the closest relative of the new species, occurs in Italy in a range of different habitats ranging from about 200 to 2000 m altitude (Lepiforum 2018; Leraut 2006). The extant ranges of *P. cantabricus* sp. n. and *P. aemilianus* may reflect the survival of isolated *Pharmacis* populations in the Iberian and Italian refugia, respectively. It appears that the Franco-Cantabric region may have been a particularly important refugium for *Pharmacis*, as two species, *P. cantabricus* sp. n. and *P. pyrenaicus* are found only here. *Korscheltellus castillanus* is likely to represent another survivor linked to the Iberian refugium. Notably, alpine refugia have been recently proposed for genetically heterogenous populations of *Hepialus humuli* (Linnaeus, 1758). However, the well-developed dispersal ability of this species appears to have prevented further diversification (Simonsen and Huemer 2014).

The restricted distribution of several of the *Pharmacis* species is likely to be supported by the limited potential for dispersal owing to the brachyptery of the females. Interestingly, it appears that brachyptery in *Pharmacis* females has arisen at least twice independently, as it can be found in the *P. carna* group, specifically in the sister species *P. anselminae* and *P. bertrandi*, and in *P. pyrenaicus*, which according to our molecular analyses belong to different clades within the genus. Although female *P. cantabricus* sp. n. have well-developed wings, they are short in comparison to the abdomen (Fig. 1), suggesting that they are unable to fly before they have laid the majority of their eggs. Thus, it appears that, similar to hepialid genera in other parts of the world (Dugdale 1994; Edwards and Green 2011), brachyptery is part of the ground plan of *Pharmacis*. It is indeed tempting to speculate that additional isolated *Pharmacis* species might be found in the mountains of southern Europe, particularly in the northern Balkans.

We have here followed the generic division of *Pharmacis* and *Korscheltellus* proposed by Viette (1949), Wagner (1988) and Grehan (2012). However, the morphological and genetic evidence for the separation of *Korscheltellus* and *Pharmacis* should be revisited. The spatulate shape of the elongated ventral extension of the pseudotegumen (trulleum *sensu* Zilli 1988 and Simonsen 2018) or meso-

Figures 32–35. Live *Pharmacis* specimens. **32.** *P. cantabricus* sp. n., mating pair, Spain, Picos de Europa. **33.** *P. carna*, mating pair, Poland, Tatra Mts. **34.** *P. anselminae*, mating pair, Italy, Valle de Aosta. **35.** *P. pyrenaicus*, female, Spain, Pyrenees. Images **33**, J. Wenta; **34**, R. Bryner; **35**, E. Beltrán.

some (*sensu* Wagner 1988 and Grehan 2012) is considered a synapomorphy of *Korscheltellus*. While the size and shape of the ventral extension of the pseudotegumen in *Korscheltellus* and *Pharmacis* species is indeed different (Figs 39, 40, 44), it is notably reduced or possibly absent in *P. pyrenaicus* (Figs 42, 43), a species that our COI sequence analysis (Fig. 4) places within *Korscheltellus*. Therefore, more extensive DNA sequence and morphological analyses are required to resolve the phylogeny of the species currently placed in *Korscheltellus* and *Pharmacis*.

Finally, the generic placement of some species from Central Asia and the Eastern Palaearctic that are currently assigned to the genus *Thitarodes* should be reassessed as they show similarities to *Korscheltellus*. This includes *T. nebulosus* (Alphéraky, 1889), a species considered to be closely related to *K. fusconebulosa* by Leraut (2006). Thus, it remains to be determined whether *Pharmacis* indeed contains only the current group of European taxa or should be expanded to contain *Korscheltellus* and perhaps additional Eastern Palaearctic hepialid taxa.

Notably, de Freina and Witt (1990) have questioned the validity of several taxa, including *P. anselminae*, *P. bertrandi* and *K. castillanus*, and suggested that they are solely representatives of isolated populations of *P. pyrenaicus*. Based on both genitalia morphology and COI analysis, this is surely not the case. *Pharmacis anselminae* and *P. bertrandi* are sister species and belong to the *P. carna* group of species, while *P. pyrenaicus* occupies an isolated position in comparison to the other species of *Pharmacis*. Although *K. castillanus* could not be studied in detail in our analysis due to the paucity of available material, it is clear that, based on external appearance and genitalia morphology (Agenjo 1942), it is not closely related to *Pharmacis* but shows affinities to species combined in *Korscheltellus*.

The hepialid fauna of Spain was last reviewed by Agenjo (1942) who illustrated the male and female genitalia of all taxa. He listed *H. humuli*, *P. pyrenaicus*, *K. fusconebulosa*, *K. castillanus*, *K. lupulina* and *Triodia sylvina* (Linnaeus, 1761), and subsequent studies did not add any new species to this list (Garcia et al. 1983; de Freina and Witt 1990). Thus, with the addition of *P. cantabricus* sp. n., the hepialid fauna of Spain now comprises seven species. Only two species appear to be known from Portugal, *K. lupulina* and *T. sylvina* (Corley, personal communication).

Notes on the species of *Pharmacis* and *Korscheltellus*

P. aemilianus (Constantini, 1911)

Figs 9, 10, 28, 40

This species is an Italian endemic, which occurs in most parts of the mainland, ranging from about 200 to 2000 m altitude (Leraut 2006; Lepiforum 2018). It was redescribed and the male genitalia were illustrated by Zilli (1988). Its flight period ranges from July to September, but most records appear to be from August (Leraut 2006; Lepiforum 2018; Mazzei et al. 2018). According to Mazzei (personal communication), in the Central Apennines the species occurs in open forest with *Quercus* and *Fagus* above 1000 m. It is attracted to light quite commonly around dusk. The males fly quickly for about half an hour, then they disappear. It has not been seen to be active during the day. Additional detailed information can be found in Bertaccini et al. (1997). Images of live males and females were published by Mazzei et al. (2018) and Lepiforum (2018).

Material examined. 1 ♂, 1 ♀, Italy, Abbruzi, Pescocostanzo (MfN, genitalia prep AK864, Figs 9, 10, 40); 1 ♂, Italy, Vado di Pezza, Rovere (L'Aquila), 23.vii.2016, image Paolo Mazzei (Fig. 28).

Figures 36–38. Live *Korscheltellus* specimens, Spain. **36–38.** *K. lupulina*, Palencia. **36.** Male. **37.** Female. **38.** *K. fusconebulosa*, Picos de Europa.

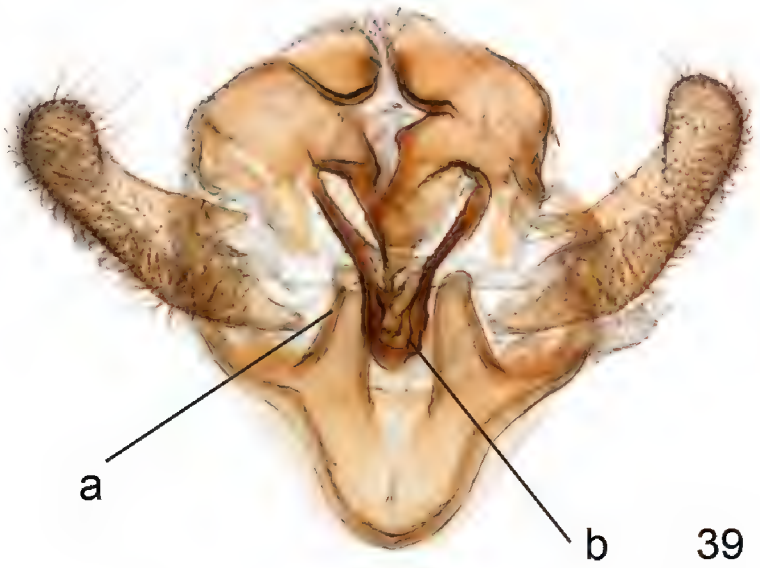
***P. pyrenaicus* (Donzel, 1838)**
Figs 11, 12, 35, 42, 43, 48

This species is endemic to the Pyrenees (Spain, France and Andorra), where it occurs at altitudes between 1800 and 2800 m (Garcia et al. 1983; de Freina 1990; Leraut 2006; Lépi'Net 2018). Leraut (2006) proposed that the taxon *alticola* Oberthür, 1881 should be considered a distinct subspecies of *P. pyrenaicus*. Male and female genitalia were illustrated by Agenjo (1942), male genitalia also by Viette (1948) and Leraut (2006). The mating behaviour and oviposition was described in detail by Bethune-Baker (1913). Images of males and females can be found on Lépi'Net (2018) and Biodiversidadvirtual (2018, as *Pharmacis* sp.).

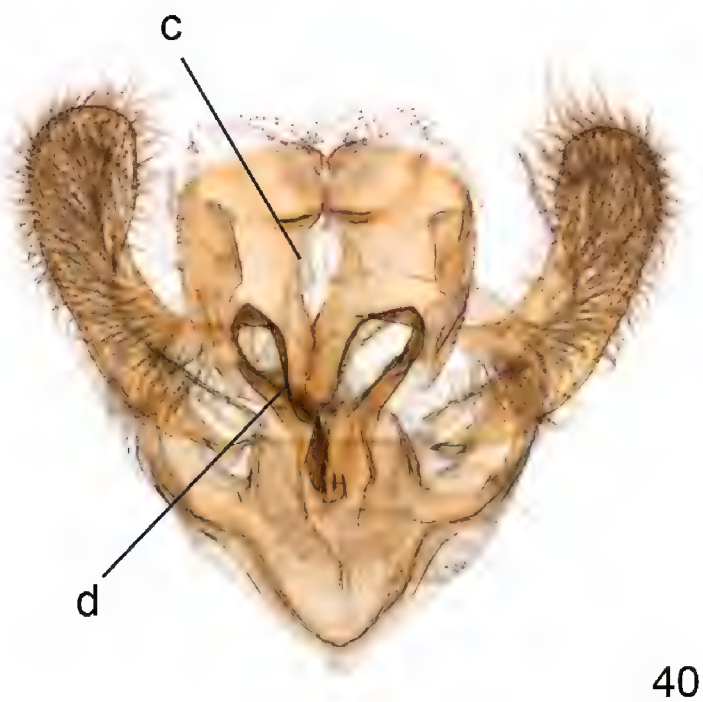
Material examined. *P. pyrenaicus pyrenaicus*: 1 ♂, France S, Pyrenees-O., Fort Rome NW, Col de Puymorens, 2000–2500 m, 13.vii.2003, leg. Andree Salk (CAK, genitalia prep. AK820, DNA AK350, Figs 11, 42, 48); 1 ♀, Spain, Huesca, Pico Turbón, 2000 m, 15.vii.2015, image Enrique Murria Beltrán (Fig. 35); 1 ♂, France, Pyr. Or., Casteil Pla Guillem, 2400 m, 2.vii.1998, 15 h, leg. Peslier (CAM); 1 ♂, France, Gourette, 2300 m, 26.vii.1994 (CAM). *P. pyrenaicus alticola*: 1 ♂, Pyren[nees]. Stgr. / genitalia prep. AK860 (MfN, genitalia prep. AK860, Figs 12, 43).

***P. bertrandi* (Le Cerf, 1936)**
Figs 13, 26

This species was described from the French Alps (Le Cerf 1936), where it has also been found more recently (Longieras 2013). It occurs at altitudes between 1800–2500 m (Leraut 2006). It was unknown in Italy (Bertaccini et al. 1997) but was recently discovered at high altitudes in the north-west of the country (Gianti and Delmastro 2006). According to Gianti and Delmastro (2006) and Longieras (2013) males fly rapidly early in the morning between 7.30 and 9.00 am. However,



39



40

41

Figures 39–41. *Pharmacis* genitalia. **39.** *P. cantabricus* sp. n., male, paratype. **40.** *P. aemilianus*, male. **41.** *P. cantabricus* sp. n., female, paratype. a – vincular condyles; b – ventral extension of the pseudotegumen; c – apical margin of pseudotegumen; d – ventral pseudoteguminal arm.

the species has only rarely been collected during the day. Recently, a large number of males was observed at Gias Valcavera (Prov. Cuneo) in Italy at about 2050 m altitude (Mayr, personal communication). The specimens were attracted to light traps between 2 am and dawn. The habitat was a mosaic of alpine pastures and scree slopes, and specimens were seen between the 17 and 27 July. In the same locality only one male was seen flying in the morning. Thus, it is possible that *P. bertrandi* flies mainly during the second half of the night and that diurnal activity is the exception. Alternatively, the flight time may depend on local conditions. The female of *P. bertrandi* is brachypterous and has only rarely been collected; one is illustrated on Lepiforum (2018). The male genitalia were illustrated by Viette (1948), Teobaldelli (1977), Gianti and Delmastro (2006) and Leraut (2006). The validity of this taxon was doubted by de Freina and Witt (1990); however, based on both morphology and barcoding results, we consider *P. bertrandi* a valid species.

Material examined. 15 ♂, Italy, Prov. Cuneo, Gias Valcavera, 2050 m, 44°22.6'N, 07°08.2'E, 23. and 27.vii.2009, 17.vii.2012, 22.vii.2013, leg. A. Mayr (CAM, CAK, Fig. 13); 1 ♀, Valle Grana, 2400 m, 15.vii.2013, leg. L. Bertoncino (CAM).

***P. carna* ([Denis & Schiffermüller], 1775)**
Figs 14–16, 27, 33

This species is distributed throughout the higher central European mountains, including the Alps and Carpathian Mts., also in Fennoscandia. Records from the Ural Mts (de Freina and Witt 1990) appear to relate to *Gazoryctra uralensis* (Anikin and Zolotuhin 2017). Within its range *P. carna* seems to occur only locally. According to Buser et al. (2000), in Switzerland the species flies in rich meadows between 1200 and 1900 m. The same authors state that the males fly after midnight and are occasionally attracted to light. According to Daniel (1950), however, the main time of activity is during daylight hours. He observed them in the German Alps at altitudes between 1150 and 2200 m, most specimens between 1700–2000 m, from early in the morning to midday, in shaded places even into the afternoon. He also observed mating and oviposition during the day. This is consistent with observations by Wenta (personal communication), who in Poland frequently observed mating in the morning. However, he never saw the males flying, suggesting that at this locality they were active during the night or very early in the morning. A female was observed laying eggs in the Jaworzynka Valley, Tatra Mts, at an altitude of about 1400 m at 11 am (Wenta, personal communication). Thus, it is likely that local conditions determine the flight time of *P. carna*.

Material examined. 1 ♂, Austria, Oberösterreich, Weyer, Küpfern, train station, 400 m, 11.vii.1999, at light, leg. E. Friedrich (CEF, Fig. 14); 1 ♂, Austria, Steiermark, Alt-Aussee, Loser, 1600 m, 5.viii.1999, at light, leg. E. Meisinger, E. Friedrich (CEF, Fig. 15); 2 ♂, Slovenia, Julische Alpen, Bovec, Mangart, 1700 m, 27.vi.2003, at light, leg. E. Friedrich (CEF); 1 ♀, Italy, Lombardia, Passo di Croce Domini, Brescia N, Astrio E, 1700–2350 m, at day, 21.-23.vii.2009, leg. Andree Salk (CAK, Fig. 16).

***P. anselminae* (Teobaldelli, 1977)**
Figs 17, 25, 34, 44, 47

This species is only known from the Aosta valley in NW Italy at altitudes between 1800 and 2500 m. It inhabits alpine meadows and pastures. Males fly rapidly in the sun, starting in the morning and continuing until late afternoon, with peak activity between 10 am and noon. They stop flying when the sun disappears behind clouds (Teobaldelli 1977; Kristal et al. 1994; Bertaccini et al. 1997; Buser et al. 2000; and observations by the first author). The male genitalia were illustrated by Leraut (2006), Kristal et al. (1994) and Teobaldelli (1977). Leraut (2006) erroneously reported that this species flies at night. The validity of this taxon was doubted by de Freina and Witt (1990); however, based on both morphology and barcoding results, we undoubtedly consider *P. anselminae* to be a valid species.

Material examined. 15 ♂, 2 ♀, Italy, Val d'Aosta, Val Valleile, Cogne, 1950 m, 11.vii.1990, leg. A. Kallies (CAK, genitalia prep. AK863, Figs 17, 44, 47).

***P. claudiae* Kristal & Hirneisen, 1994**
Fig. 18

This species was described relatively recently from the Aosta Valley in north-western Italy (Kristal et al. 1994). It is related and similar to *P. carna*, but it differs in details of the wing markings, antennae, and genitalia (Kristal et al. 1994; Buser et al. 2000). The males fly for about two hours, starting just before midnight. The species occurs in alpine grasslands at altitudes of 1900–2600 m in the Valle d'Aosta in north-western Italy. The flight period is from mid-July to early August (Kristal et al. 1994; Buser et al. 2000). The fully winged female was described by Bertaccini et al. (1997). The male genitalia were illustrated by Kristal et al. (1994). Images of live adults were published by Mazzei et al. (2018) and Lepiforum (2018).

Material examined. 1 ♂, Italy, Val d'Aosta, Valtourrenche, A.-St. Andre, Torgnon, Alpi Clogne, 2100–2200m, 25.vii.1994, leg. P.M. Kristal & J. Roth (CAK, Fig. 18).

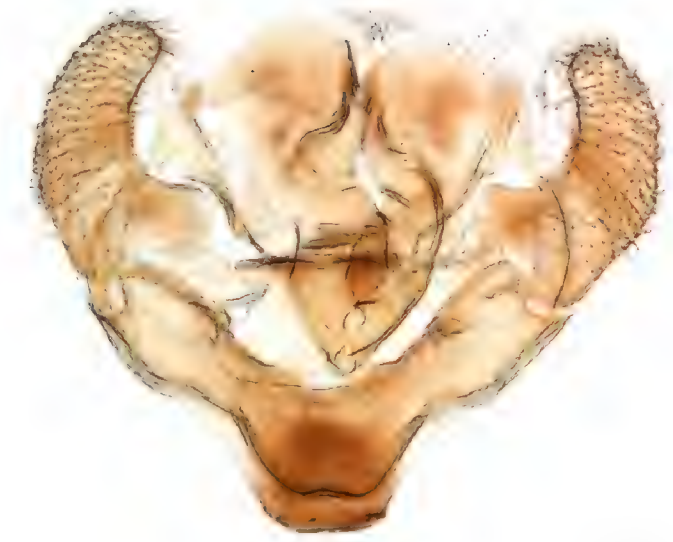
***K. fusconebulosa* (De Geer, 1778)**
Figs 19–21, 38

This species is widespread and occurs from Western Europe to Japan (Leraut 2006). It is well recorded from the northern part of Spain (Garcia et al. 1983; Ylla and Masó 1990).

Material examined. 1 ♂, Germany, Schmalkalden, JH 'Ebertswiese', 730 m, at light, 30.vi.–2.vii.1989, leg. E. Friedrich (CEF, Fig. 20); 1 ♀, same locality, 16.vi.1993, at light, leg. E. Friedrich (CEF, Fig. 21); 1 ♂, Germany, Niesky, Niederspree, at light, 16.vi.1998, leg. E. Friedrich (CEF); 1 ♂, Germany, Mecklenburg, Umg. Schwerin, Lewitzwald, Friedrichsmoor, 20.vi.1990, at light, leg. A. Kallies (CAK); 1 ♀, Italy, Lombardia, Passo di Crocce Domini, Brescia N, Astrio E, 1700–2350 m, 21.–23.vii.2009, leg. A. Salk (CAK); 1 ♂, Italy, Vinschgau, N Laas, Allitz-Säge, 1400 m, at light, 3.vii.2006, leg. E. Friedrich (CEF, Fig. 19); 1 ♀, Germany, Oberweissbach, Meuraer Heide, 28.vi.1996, at light, leg. E. Friedrich (CEF); 1 ♂, Spain, Aran, Tredós, 23.vi.2018, leg. et coll. A. & Z. Laštůvka; 1 ♀, Spain, Cantabria, Fuenfría, 26.v.2006, image Teresa Farino; 1 ♂, Spain, Cantabria, Cantera de Vendejo, 26.v.2014, image Teresa Farino (Fig. 38).

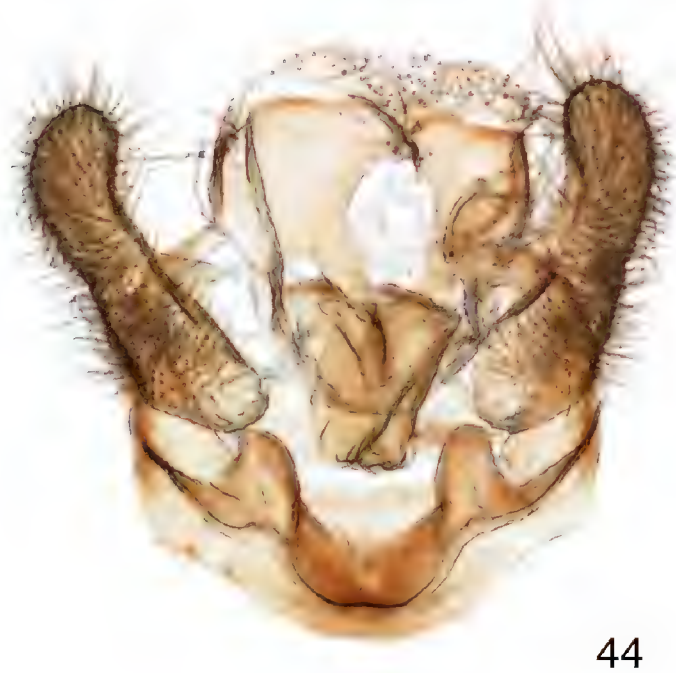
***K. castillanus* (Oberthür, 1883), stat. rev., comb. n.**
Fig. 22

This taxon is insufficiently known. It was treated as a member of the genus *Pharmacis* by de Freina and Witt (1990) and Nielsen et al. (2000). Later, Leraut (2006) examined the holotype and the male genitalia and considered *castillanus* a subspecies of *K. fusconebulosa*. A close relationship between *castillanus* and *K. fusconebulosa* is supported by the presence of a spatulate ventral projection of the pseudotegumen in the male genitalia, the autapomorphic character of *Korscheltellus*, and the similarity of the two taxa in forewing pattern. However, we do not see sufficient evidence for the notion that *castillanus* should be considered a subspecies of *K. fusconebulosa*. Thus, we here formally transfer *castillanus* to *Korscheltellus* and retain it as a valid species. In line with our view, Agenjo (1942), who illustrated the male and female

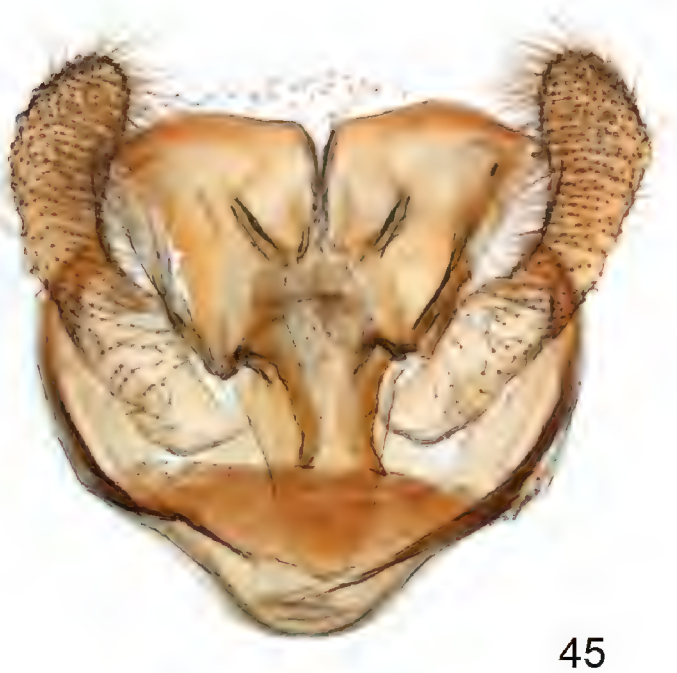


42

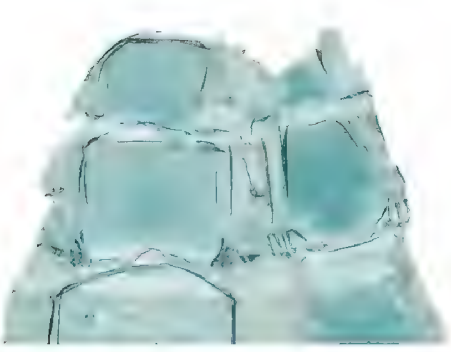
43



44



45



46

47

48

Figures 42–48. *Pharmacis* and *Korscheltellus*, male genitalia (**42–45**) and terminal abdominal sclerites (**46–48**). **42.** *P. pyrenaicus pyrenaicus* (pseudotegumen flattened). **43.** *P. pyrenaicus alticola* (pseudotegumen in natural position). **44.** *P. anselminae*. **45.** *K. lupulina*. **46.** *P. cantabricus* sp. n. paratype (stained). **47.** *P. anselminae* (unstained). **48.** *P. pyrenaicus pyrenaicus* (unstained). Images **46–48**, Q. Wang.

genitalia of both taxa in considerable detail, treated both taxa as distinct species. Further work, in particular detailed morphological and molecular studies are required to clarify the status of *K. castillanus*.

Korscheltellus castillanus is similar to *K. fusconebulosa* but smaller and less vividly coloured, with the wingspan ranging from 27–28 mm in males to 32 mm in females (males 28–35 mm, females 35–46 mm in *K. fusconebulosa*). According to the figures provided by Agenjo (1942) the sub-basal costal tooth at the ventral edge of the valva is less developed in *K. castillanus* compared to *K. fusconebulosa.* Furthermore, the valva is narrower and the saccus much less extended in *K. castillanus* compared to *K. fusconebulosa.*

K. castillanus is known from only a small number of specimens that have been collected in a small area north-west of Madrid (La Granja de San Ildefonso, Balsain, El Escorial, in the Sierra de Guadarrama), and no new material has been found in the last 70 years. According to Agenjo (1942), *K. castillanus* flies between May and July.

Material examined. 1 ♀, [Spain] Sn Ildef [San Ildefonso], 84, m / 1/6 / ♀ [unreadable] Stgr. (MfN, Fig. 22).

K. gracilis (Grote, 1865)

This is a North American species, which has been discussed in detail elsewhere (Wagner 1988; Wagner and Rosovsky 1991; Grehan 2012). Previous morphological studies have suggested a close relationship with *K. fusconebulosa* (Wagner 1988; Grehan 2012), which is confirmed here based on our COI study.

K. lupulina (Linnaeus 1758)

Figs 23, 24, 36, 37, 45

This species is widespread in Europe and well recorded from the northern part of Spain (Garcia et al. 1983; Ylla and Masó 1990).

Material examined. 1 ♂, Spain, Leon, La Una, 15.vi.2013, leg. González Estébanez (CAK, genitalia prep. AK816, Fig. 45); 1 ♀, Spain, Palencia, Villaescusa de las Torres, 5.vi.2013, image Teresa Farino; 1 ♂, Spain, Palencia, Arroyo Lazán, 3.vi.2013, image Teresa Farino (Fig. 36, coll Marc Botham); 1 ♀, Spain, Palencia, Puerto de Piedrasluengas, 27.v.2015, image Teresa Farino (Fig. 37); 1 ♂, S France, Ardeche, Lagorce, Ibie valley, 11–17.ix.1993, leg. D. Forster (CAK, Gen. prep. AK817); 1 ♀, Austria, Steiermark, Gosdorf/Mur, 16.v.1993, during day, leg. D. Hamborg (CAK, Fig. 24); 2 ♂, 1 ♀, Germany, Thuringia, Jena, Neulobeda-West, 19–31.v.1989, leg. E. Friedrich (CEF, Fig. 23); 1 ♀, Germany, Thuringia, Jena, Kernberge, 7.v.1980, leg. E. Friedrich (CEF).

Acknowledgements

We would like to express our gratitude to the large number of individuals who have contributed to this work. Only through their support was this study made possible in its current form. We thank John Grehan for alerting the first author to the images of *P. cantabricus* sp. n., and thereby initiating this study. We thank Yeray Monasterio León, Ruth Escobés Jiménez and Félix Javier González Estébanez for their invaluable help in observing and collecting type specimens of *P. cantabricus* sp. n. We thank Joël Minet, Vadim Zolotuhin, John Grehan, Axel Steiner, Thomas Witt and Josef de Freina for information regarding type material and for help collating relevant literature. We express our gratitude to Andree Salk and Tony Mayr for donating

material used in this study. We thank Antoine Longieras, Mauro Gianti, Giovanni Delmastro and Tony Mayr for information concerning the distribution and habits of *P. bertrandi*, Antoine Longieras, Rudolf Bryner and Helmut Deutsch for permission to use their images, Enrique Murria Beltrán for images and specimens of *P. pyrenaicus*, Jarosław Wenta for images and information relating to *P. carna*, Paolo Mazzei for images and information relating to *P. aemilianus*, Egbert Friedrich for images, and Yeray Monasterio León, Marcos Toribio, Colin W. Plant, Zdeněk Laštůvka, Martin F. V. Corley and Roger Vila for information concerning the distribution of Iberian Hepialidae. We are grateful to Axel Hausmann and Peter Huemer for providing sequences used in this study, and to Wolfram Mey for access to type material under his care. Furthermore, we wish to thank Tom McConville and Liz Milla for performing COI sequencing and analysis, and Qike Wang for his help with imaging. We would like to thank John Grehan, Thomas Simonsen and Carlos Mielke for helpful comments on the manuscript. Finally we would like to thank the Consejería de Medio Rural, Pesca y Alimentación del Gobierno de Cantabria and the Parque Nacional de Picos de Europa for providing us with the necessary licences to carry out the field work.

References

Agenjo R (1942) *Hepialus* de España (Lep. Hep.), EOS 18: 145–175. [pls 3–6] http://hdl.handle.net/10261/148148

Anikin VV, Zolotuhin VV (2017) Types of Bombyces and Sphinges described from the Volgo-Ural Region. Proceedings of the Museum Witt Munich 7: 506–514, 644. [plate 52]

Bertaccini E, Fiumi G, Provera P (1997) Bombici e sfingi d'Italia (Lepidoptera Heterocera). Vol. 2. Natura, Guiliano Russo Editore, Menterenzio (BO), 256 pp.

Bethune-Baker GT (1913) The pairing habits of *Hepialus pyrenaicus*. The Entomologist's Record and Journal of Variation 25(2): 52–53.

Biodiversidadvirtual (2018) Biodiversidadvirtual. http://www.biodiversidadvirtual.org/insectarium/Superfamilia-Hepialoidea-cat23577.html [Accessed 18 July 2018]

Buser H, Huber W, Renato J (2000) Hepialidae. In: Fotorotar AG (Ed.) Schmetterlinge und ihre Lebensräume (Vol. 3). Pro Natura – Schweizerischer Bund für Naturschutz, Druck, Verlag, Neue Medien, 61–69.

Daniel F (1950) Beobachtung über die Lebensweise hochalpiner Vertreter der Gattung *Hepialus*. Mitteilungen der Münchener Entomologischen Gesellschaft 40: 203–206. https://www.zobodat.at/pdf/MittMuenchEntGes_040_0203-0206.pdf

de Freina JJ, Witt TJ (1990) Die Bombyces und Sphinges der Westpalaearktis. Vol. 2. Edition Forschung und Wissenschaft, München, 143 pp.

Dugdale JS (1994) Hepialidae (Insecta: Lepidoptera). Fauna of New Zealand 30. Manaaki Whenua Press, Lincoln, 136 pp.

Edwards ED, Green K (2011) Two new species of *Oxycanus* Walker (Lepidoptera: Hepialidae) from Kosciuszko National Park, one with a sub-brachypterous female. Australian Journal of Entomology 50: 78–85. https://doi.org/10.1111/j.1440-6055.2010.00790.x

Garcia AG, Llorca JJ, Planasa AM, De-Gregorio JJP, Ferrer-Vidal IR (1983) Revisió de la família Hepialidae Stephens, 1829 (Lepidoptera: Homoneura) a Catalunya. Butlletí de la Institució Catalana d'Història Natural 49 (Sec. Zool. 5): 111–117. https://www.raco.cat/index.php/ButlletiICHN/article/viewFile/233040/315108

Gianti M, Delmastro GB (2006) Prime Notizie Sulla Presenza in Territorio Italiano di *Pharmacis bertrandi* (Le Cerf, 1936) (Lepidoptera, Hepialidae). Rivista Piemontese di Storia Naturale 27: 133–141.

Grehan JR (2012) Evidence for the generic placement of the ghost moth *Korscheltellus fusconebulosa* (De Geer, 1778) (Lepidoptera: Hepialidae) and comments on the monophyly of *Korscheltellus* Börner, 1920. Bulletin of the Buffalo Society of Natural Sciences 41: 29–32.

Jiang N, Li XX, Li QP, Li WJ, Han H-X (2016) *Thitarodes* Viette, 1968: a new generic synonym and a new species from China (Lepidoptera: Hepialidae). SHILAP Revista de Lepidopterologica 44(175): 373–378. http://www.redalyc.org/html/455/45549999002/

Kandul NP, Lukhtanov VA, Dantchenko AV, Coleman JWS, Sekercioglu CH, Haig D, Pierce NE (2004) Phylogeny of *Agrodiaetus* Hübner, 1822 (Lepidoptera: Lycaenidae) inferred from mtDNA sequences of COI and COII and nuclear sequences of EF1-α: karyotype diversification and species radiation. Systematic Biology 53(2): 278–298. https://doi.org/10.1080/10635150490423692

Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kristal PM, Hirneisen N, Steiner A (1994) Eine weitere endemische Hepialidae aus den Alpen: *Pharmacis claudiae* sp. n. (Lepidoptera: Hepialidae). Nota Lepidopterologica 17: 53–72.

Le Cerf F (1936) Une hépiale nouvelle de France (Lep. Hepialidae), Bulletin de la Société Entomologique de France 41: 290–292.

Lépi'Net (2018) Les carnets du lépidoptériste français. http://www.lepinet.fr/especes/nation/lep/index.php?e=&id=00250# [Accessed 1. April 2018]

Lepiforum (2018) Bestimmungshilfe für die in Europa nachgewiesenen Schmetterlingsarten. http://www.lepiforum.de/lepiwiki.pl [Accessed 1. April 2018]

Leraut P (2006) Moths of Europe. Volume 1: saturnids, lasiocampids, hawkmoths, tiger moths. NAP Editions, Verrières-le-Buisson, 392 pp.

Longieras A (2013) Nouvelles observations de *Pharmacis bertrandi* (Le Cerf, 1936) dans le Haut-Queyras (Hautes-Alpes). Alexanor 25(6): 355–360.

Mazzei P, Morel D, Panfili R (2018). Moths and Butterflies of Europe and North Africa. http://www.leps.it/indexjs.htm?SpeciesPages. [Accessed 1. April 2018]

Milla L, Nieukerken EJ van, Vijverberg R, Doorenweerd C, Wilcox SA, Halsey M, Young DA, Jones T, Kallies A, Hilton DJ (2017) A preliminary molecular phylogeny of shield-bearer moths (Lepidoptera: Adeloidea: Heliozelidae) highlights rich undescribed diversity. Molecular Phylogenetics and Evolution 120: 129–143. https://doi.org/10.1016/j.ympev.2017.12.004

Nielsen ES, Robinson GS, Wagner DL (2000) Ghost-moths of the world: a global inventory and bibliography of the Exoporia (Mnesarchaeoidea and Hepialoidea) (Lepidoptera). Journal of Natural History 34: 823–878. https://doi.org/10.1080/002229300299282

Pentinsaari M, Salmela H, Mutanen M, Roslin T (2016) Molecular evolution of a widely-adopted taxonomic marker (COI) across the animal tree of life. Scientic Reports 6: 35275. https://doi/org/10.1038/srep35275

Simonsen TJ (2018) Splendid ghost moths and their allies. A revision of Australian *Abantiades*, *Oncopera*, *Aenetus*, *Archaeoaenetus* and *Zelotypia*. Monographs on Australian Lepidoptera 12: 1–312.

Simonsen TJ, Huemer P (2014) Phylogeography of *Hepialus humuli* (L.) (Lepidoptera: Hepialidae) in Europe: short distance vs. large scale postglacial expansions from multiple Alpine refugia and taxonomic implications. Insect Systematics & Evolution 45: 209–249. https://doi/org/10.1163/1876312X-44032104

Stamatakis A (2014) RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Teobaldelli A (1977) Eine neue *Hepialus*-Art aus Italien. Nachrichtenblatt der bayerischen Entomologen 26: 38–43.

Viette P (1949) Contribution à l'étude des Hepialidae. 12e note Genres et synonymie. Lambillionea 49: 101–104.

Wagner DL (1988) Taxonomic status of *Korscheltellus* Börner in North America (Lepidoptera: Hepialidae). Journal of the New York Entomological Society 96: 53–54. https://www.jstor.org/stable/25009697

Wagner DL, Rosovsky J (1991) Mating systems in primitive Lepidoptera with emphasis on the reproductive behaviour of *Korscheltellus gracilis* (Hepialidae). Zoological Journal of the Linnean Society 102: 277–303. https://doi.org/10.1111/j.1096-3642.1991.tb00003.x

Wilke T, Schultheiß R, Albrecht C (2009) As time goes by: a simple fool's guide to molecular clock approaches in invertebrates. American Malacological Bulletin 27: 25–45. https://doi.org/10.4003/006.027.0203

Ylla J, Masó A (1990) Estudi de les poblacions ibèriques de *Korscheltellus lupulinus* Linnaeus, 1758 (Lepidoptera: Hepialidae). Sessió Conjunta d'Entomologia 6(1989): 119–130. https://www.raco.cat/index.php/SessioEnto/article/view/246653

Zilli A (1988) Un endemismo appenninico misconosciuto: *Hepialus aemilianus* Constanti, 1911. Bollettino della Società entomologica italiana, Genova 120(1): 43–48.

Zou ZW, Liu X, Zhang GR (2010) Revision of taxonomic system of the genus *Hepialus* (Lepidoptera: Hepialidae) currently adopted in China. Journal of Hunan University of Science & Technology (Natural Science Edition) 25(1): 114–120. [In Chinese, with English abstract]